Do the New Zealand divaricates defy Corner's rules?

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Divaricate plants are a collection of New Zealand shrubs and tree juvenile forms with interlaced branches bearing leptophylls to nanophylls. Although the divaricate form has attracted much attention from ecologist and botanists, it is not clear to what extent divaricate plants depart from usual patterns of plant allometry. Here, we explore the relationship between twig and leaf size in a set of 11 divaricate species and 13 non-divaricate congeners, as a test of one of Corner's rules: the axial conformity rule. This rule states that stouter branches should bear larger and more complex leaves, a pattern that has been widely observed throughout the world. The non-divaricate species we examined conformed to the expected positive relationship between twig diameter and leaf area. In contrast, there was no correlation between these two variables among divaricate species: there was no significant trend in leaf size across a three-fold range of twig diameter. These results support qualitative field observations, and conducting this work suggested that testing Corner's second rule (the greater the ramification, the smaller the branches and appendages) might be compromised by the difficulty of finding a suitable protocol for accurately measuring the degree of ramification in divaricate and non-divaricate species.

Keywords: Corner's rules; divaricating shrubs; functional traits; New Zealand; plant architecture; structural plant defences

Introduction

Divaricate plants are a striking feature of the New Zealand flora (Wardle 1991), with their characteristic cage-like architecture of usually stiff, tangled branches bearing lepto- to nanophylls leaves (Raunkiær 1934) and branching at wide angles (on average > 70°, and sometimes > 90°, Bulmer 1958; Greenwood & Atkinson 1977). This habit is found in as many as 80 eudicot and one conifer species, representing 20 families (Maurin & Lusk 2020). Most divaricates are shrubs or small trees that remain divaricate their whole life, although there are 11 heteroblastic tree species that have a divaricate juvenile phase before assuming a more typical growth form as adults (Maurin & Lusk 2020). Ecologists

and botanists have long debated the origin of this unusual growth form and the causes of its remarkable abundance in New Zealand (e.g. Greenwood & Atkinson 1977; McGlone & Webb 1981; Atkinson & Greenwood 1989; Bond et al. 2004; Lusk et al. 2016), with similar-looking plant being much less common in most other regions of the world (reviewed by Maurin & Lusk 2020).

One question not so far addressed is whether the divaricate form departs from usual patterns of plant allometry. Studying the morphological properties of fruits and seeds of tropical plants, Corner (1949) proposed a set of morphological features that the immediate ancestors of all flowering plants likely displayed. From these traits he derived covariation patterns, now known as "Corner's rules", that he explained this way (p. 390):

1. "Axial conformity. The stouter, or more massive, the axis in a given species, the larger and more complicated are its appendages".
2. "Diminution on ramification. The greater the ramification, the smaller become the branches and their appendages".

These rules have been studied on an interspecific level, showing that the vast majority of the species examined worldwide conform to these two rules (reviewed by Olson et al. 2018). However, our field observations suggest that not all divaricate plants may follow these rules. Some divaricates appear to have relatively stout branches compared to the size of their leaves, especially in exposed environments, and even high-order branches in distal parts of their crowns remain stout—similar "antler" branching has been noted in plants of open environments in other regions (Tucker 1974; Halloy 1990). The most striking examples are some species of *Melicytus* J.R.Forst. & G.Forst. (e.g. *M. alpinus* (Kirk) Garn.-Jones and *M. crassifolius* (Hook.f.) Garn.-Jones) and *Pittosporum* Banks ex Sol. (e.g. *P. anomalum* Laing & Gourlay and *P. rigidum* Hook.f.). To our knowledge, however, there have been no quantitative comparisons of the conformity of divaricate and non-divaricate New Zealand plants to Corner's rules.

Here, we present such a comparison. We measured leaf and stem dimensions on a set of divaricate and non-divaricate congeners to test their congruity with Corner's first rule (axial conformity). We used standardised major axis (SMA) analyses to examine the relationship between the diameter of an internode (representing its stoutness) and the area of the leaves it bears, which were the only appendages present in the case of our samples.

Material and methods

We randomly chose five leaf-bearing internodes in the distal 15 cm of the crown of 1 to 3 individuals of 24 New Zealand native species of *Coprosma* J.R.Forst. & G.Forst., *Melicytus*, *Pittosporum* and *Sophora* L. on the campus of the University of Waikato (Table 1). 11 species were divaricates, and the 13 non-divaricate species encompassed a wide range of leaf lamina area (from an average of ca. 46 mm^2 to ca. 7,900 mm^2). The diameter of each internode was measured at the mid-point; their length was also recorded, although we did not analyse it in this study. For *Coprosma*, *Melicytus* and *Pittosporum*, which have entire leaves, leaf area was approximated non-destructively as an ellipse from the length and maximum width of the lamina (area = π x length/2 x width/2) of one leaf per internode. For *Coprosma* species, which have an opposite phyllotaxy, we doubled the area of this leaf (which was chosen randomly from the pair) for the statistical analyses. For *Sophora* species, which have alternate compound leaves, we collected terminal shoots and took a picture of them pressed under a clear glass pane (to flatten their leaflets), with graph paper as a scale; we then measured the area of the leaflets and internode length and mid-point diameter from the pictures using ImageJ (Schneider et al. 2012), and summed the area of the leaflets as lamina area for the analyses. A sketch providing a visual aid on how these measurements were taken is provided in Appendix 1. In all cases we made sure that

Table 1. List of the 24 species used in this study, with mean ± standard deviation of the measurements we performed. ND = non-divaricate, D = divaricate. Total lamina area of internode = area of the leaf at the internode for species with alternate phyllotaxy and entire leaves (*Melicytus*, *Pittosporum*), 2x the area of one leaf at the internode for species with opposite phyllotaxy and entire leaves (*Coprosma*), sum of the area of all the leaflets of the leaf at the internode for species with alternate phyllotaxy and compound leaves (*Sophora*); see Appendix 1 for a visual aid on how these measurements were taken. The internode length, although not used in this study, was added to provide data to back up a claim often made by authors discussing divaricate species but poorly supported because of the paucity of published quantitative measurements (Maurin & Lusk 2020): divaricates have relatively long internodes compared to the size of their leaves (not including short-shoots).

Family	Species	Species code in Fig. 1	Number of individuals sampled	Architectural group	Internode length (mm)	Mid-internode diameter (mm)	Total lamina area of internode (mm^2)
Rubiaceae	*Coprosma grandifolia* Hook.f.	COPgra	1	ND	33 ± 13	3.96 ± 0.11	7889 ± 1341
	Coprosma pedicellata Molloy, de Lange & B.D.Clarkson	COPped	1	D	4 ± 1	0.87 ± 0.15	21 ± 4
	Coprosma propinqua A.Cunn.	COPpro	1	D	9 ± 3	0.78 ± 0.06	41 ± 10
	Coprosma repens A.Rich.	COPrep	2	ND	27 ± 10	2.91 ± 0.49	2359 ± 1219
	Coprosma rhamnoides A.Cunn.	COPrha	2	D	10 ± 3	0.79 ± 0.12	60 ± 25
	Coprosma rigida Cheeseman	COPrig	1	D	27 ± 9	0.88 ± 0.12	67 ± 20
	Coprosma robusta Raoul	COProb	2	ND	43 ± 10	3.19 ± 0.62	2648 ± 810
	Coprosma wallii Petrie in Cheeseman	COPwal	1	D	9 ± 2	1.07 ± 0.21	39 ± 8
Violaceae	*Melicytus crassifolius* (Hook.f.) Garn.-Jones	MELcra	2	D	5 ± 1	2.33 ± 0.28	28 ± 14
	Melicytus micranthus (Hook.f.) Hook.f.	MELmic	3	D	10 ± 3	0.98 ± 0.20	28 ± 16
	Melicytus ramiflorus J.R.Forst. & G.Forst.	MELram	3	ND	7 ± 2	1.98 ± 0.35	1878 ± 1069
Pittosporaceae	*Pittosporum anomalum* Laing & Gourlay	PITano	2	D	6 ± 2	1.53 ± 0.35	12 ± 4
	Pittosporum cornifolium A.Cunn.	PITcor	1	ND	16 ± 9	1.47 ± 0.20	327 ± 86
	Pittosporum crassifolium Banks & Sol. ex A.Cunn.	PITcra	1	ND	7 ± 2	2.95 ± 0.46	762 ± 364
	Pittosporum ellipticum Kirk	PITell	1	ND	4 ± 1	1.57 ± 0.32	918 ± 520
	Pittosporum kirkii Hook.f. ex Kirk	PITkir	1	ND	16 ± 7	3.99 ± 0.59	1268 ± 147
	Pittosporum obcordatum Raoul	PITobc	3	D	8 ± 3	1.09 ± 0.26	24 ± 10
	Pittosporum pimeleoides A.Cunn. ex Putt. subsp. pimeleoides	PITpimpim	1	ND	10 ± 4	1.13 ± 0.29	46 ± 20
	Pittosporum pimeleoides subsp. majus (Cheeseman) R.C.Cooper	PITpimmaj	1	ND	10 ± 4	1.42 ± 0.15	75 ± 28
	Pittosporum tenuifolium Sol. ex Gaertn.	PITten	1	ND	9 ± 6	1.37 ± 0.56	710 ± 378
	Pittosporum turneri Petrie	PITtur	3	D	6 ± 3	0.79 ± 0.15	22 ± 9
Leguminosae	*Sophora chathamica* Cockayne	SOPcha	1	ND	5 ± 4	2.77 ± 0.60	1742 ± 225
	Sophora longicarinata G.Simpson & J.S.Thomson	SOPlon	1	ND	24 ± 18	2.00 ± 0.32	439 ± 90
	Sophora prostrata Buchanan	SOPpro	1	D	14 ± 2	1.36 ± 0.18	47 ± 9

the leaf we measured was attached directly to an internode of a main branch, and not to a short-shoot (i.e. a cluster of leaves resulting from a sequence of very short internodes that are often borne in lieu of or alongside leaves in divaricate species; Tomlinson 1978)—short-shoots have virtually no branch length, and would therefore need a very particular and careful treatment which is not pertinent in our study of Corner's first rule. Most plants were growing in semi-shaded conditions in a shadehouse, but to expand our dataset we also included individuals growing in similar partially-shaded environments around the campus. Non-ImageJ measurements were made with a digital calliper. All measurements were made in March to April (early autumn in New Zealand), in 2019 and 2020.

We conducted our statistical analyses in R version 3.6.1 (R Core Team 2019). We used standardized major axis (SMA) analyses to determine whether the slope and elevation of the relationship between leaf area and internode diameter differed between divaricate and non-divaricate species. Major axis is appropriate when we are interested in describing the slope of bivariate scaling relationships, rather than in predicting one variable from another (Smith 2009). The choice of only four genera was made to limit the influence of a putative phylogenetic signal on the results. We used the package SMATR version 3.4-8 (Warton et al. 2018). We $\log_{10}$-transformed the variables then worked with their average per species. The distribution of the residuals, provided in Appendix 2, (1) did not show a particular pattern when they were plotted against fitted values and (2) was reasonably close to a straight line in a normal quantile plot (QQ plot), which satisfied the assumptions of the SMA analyses.

Results

SMA showed that divaricate and non-divaricate species differed significantly in the slope of the relationship between twig diameter and leaf area (p-value = 0.049). Notably, the slopes of these relationships have opposite signs: positive for non-divaricate species (95% confidence interval: [2.22,4.83]), negative for divaricate species (95% confidence interval: [-2.98,-0.78]; Fig. 1). However, while the correlation between twig diameter and leaf area was significant in non-divaricate species (p-value = 0.001), it was non-significant in divaricate species (p-value = 0.36).

We ran another SMA analysis to gauge how the above result was leveraged by two species that might be considered outliers. *Melicytus crassifolius* and *Pittosporum anomalum* have especially thick internodes relative to the size of their leaves, compared to the bulk of the other divaricate species. We therefore repeated the SMA analysis after removing these two species from the dataset: the tests for a different slope and elevation were non-significant (respective p-values = 0.46 and 0.34) while the test for a shift along a common slope was highly significant (p-value = 4.81×10^{-10}), suggesting that the remaining species of both architectural groups fall along the same fitted relationship between twig diameter and leaf area (Falster et al. 2006). This fitted relationship was moreover highly significant (p-value = 1.22×10^{-8}). However, the correlation between twig diameter and leaf area of the remaining nine divaricate species was even less significant than when *M. crassifolius* and *P. anomalum* were included (p-value = 0.87).

Discussion

SMA showed that the non-divaricate species we considered conform to Corner's rule of axial conformity—the thicker the twig, the bigger the leaves it bears (Fig. 1). Surprisingly, there was no evidence of a relationship between twig diameter and leaf size in the divaricate species as a group; we would expect a correlation, even if differing in slope or elevation from that seen in the non-divaricate species, given the ubiquity of Corner's first rule (reviewed by Olson et al. 2018). This result however depends on the set of divaricate species included in the SMA

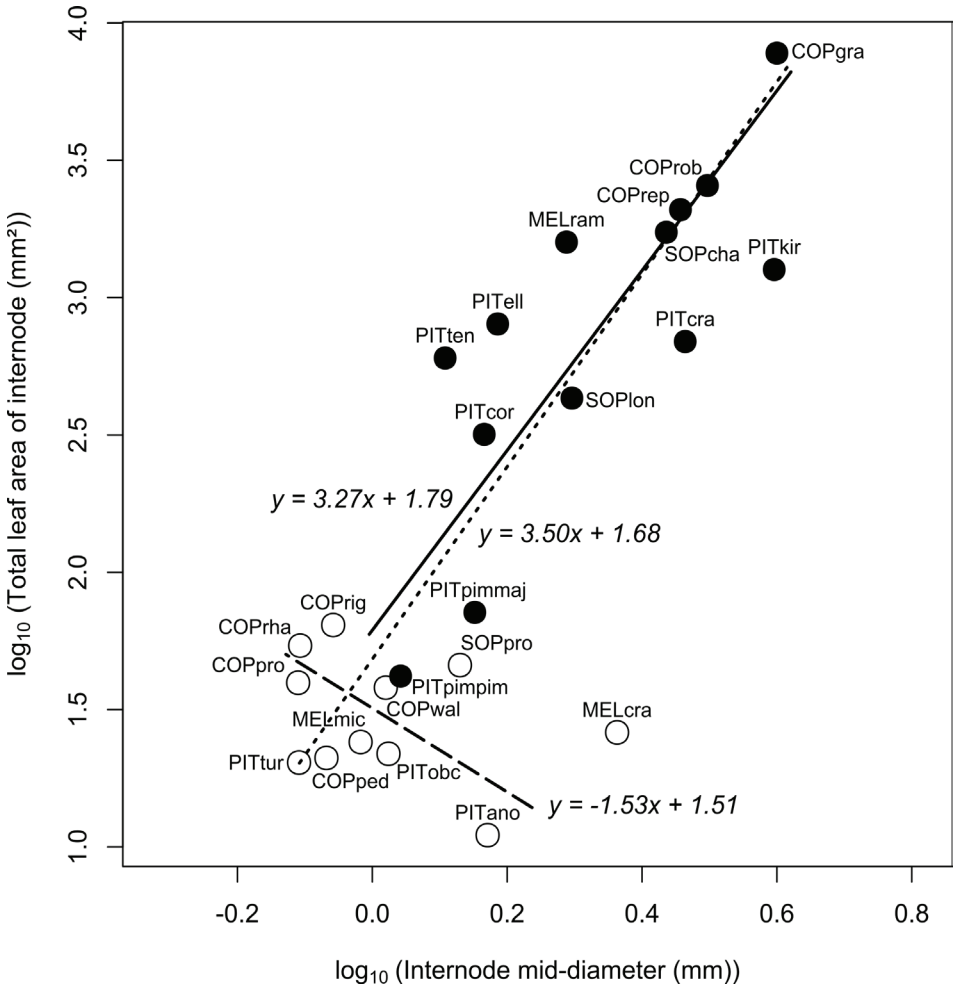

Figure 1. Scaling of the total leaf area of an internode to its diameter (log_{10}-transformed data). Empty circle = divaricate species; filled circle = non-divaricate species. Dashed line = SMA line for divaricate species, with its equation (the relationship is not significant in this case); solid line = SMA line for non-divaricate species, with its equation; dotted line = SMA line for all species with MELcra and PITano removed from the analysis, with its equation. See Table 1 for the name of the species corresponding to the codes.

analysis: if *Melicytus crassifolius* and *Pittosporum anomalum* are removed from the dataset, SMA finds that divaricate and non-divaricate species fall on the same slope showing a positive correlation between leaf and twig size, despite the lack of such a correlation among the divaricate species only. *Melicytus crassifolius* and *Pittosporum anomalum* are thus responsible for the (non-significant) negative correlation between leaf and twig size in our set of 11 divaricates. As here we report data from only about 14% of the number of species falling on the divaricate spectrum of architectures (Maurin & Lusk 2020), data from more may help clarify the nature of twig-leaf allometry in divaricate plants.

Our results reflect considerable morphological and architectural heterogeneity among New Zealand divaricate plants (Tomlinson 1978). Although the majority of the divaricate species examined did not depart significantly from the twig-leaf allometry

of their non-divaricate congeners, the two thickest-stemmed divaricate species (*Melicytus crassifolius* and *Pittosporum anomalum*) lay well outside the main data envelope (Fig. 1). This was also true to a lesser extent of *Sophora prostrata* Buchanan, the species with the next largest twig diameters. All three of these species are typical of relatively open, non-forest environments where they are exposed to harsh climatic conditions. *M. crassifolius* often grows on windswept coasts where it is exposed to salt spray (Wardle 1991), *P. anomalum* is typical of alpine and subalpine scrub (Wardle 1978; Williams 1993), and *S. prostrata* is usually reported from low scrub in semi-arid districts of the eastern South Island or on cliffs (Heenan et al. 2001). Thick stems and unusually small leaf areas may reflect adaptations to these harsh environments, with more conventional allometries being associated with more mesic environments (cf. Gleason et al. 2013).

Systematic comparisons of leaf and twig dimensions across a range of environments is recommendable for future studies. Our specimens grew in semi-shaded areas mostly well protected from wind, conditions known to sometimes relax the divaricate habit compared to areas continuously exposed to full sunlight and/or strong winds (Philipson 1963; Christian et al. 2006; pers. obs.). McGlone & Webb (1981), however, note that the degree of relaxation of the divaricate form in the shade varies considerably across species. Comparing the manifestation of Corner's first rule in individuals growing in both shaded/sheltered and sunlit/exposed conditions could provide quantitative insight into the effect of microclimate on the expression of the divaricate habit. This may advance our understanding of the evolution of these peculiar species, which has been a hotly debated topic since the late 1970s (reviewed by Maurin & Lusk 2020).

We could not assess whether our chosen divaricate species conform to Corner's second rule, the rule of diminution on ramification. It was very challenging to evaluate the branching order of the internodes we considered, because the high branching density and interlacement of most of the plants we used made it very difficult to reliably follow the main axis down to the base of the trunk. A solution would have been to consider the branching order of the internodes from the base of the distal 15 cm of branch we considered in our measurements. However, this would have posed a problem when comparing the divaricates to their non-divaricate relatives, because the non-divaricate plants we observed sometimes did not branch in these distal 15 cm; sub-sampling such trees and shrubs could artificially skew their values of branching order towards low numbers, which might mask some degree of variation between species—unless maybe a sensible sub-sampling technique is designed for such measurements.

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Disclosure statement

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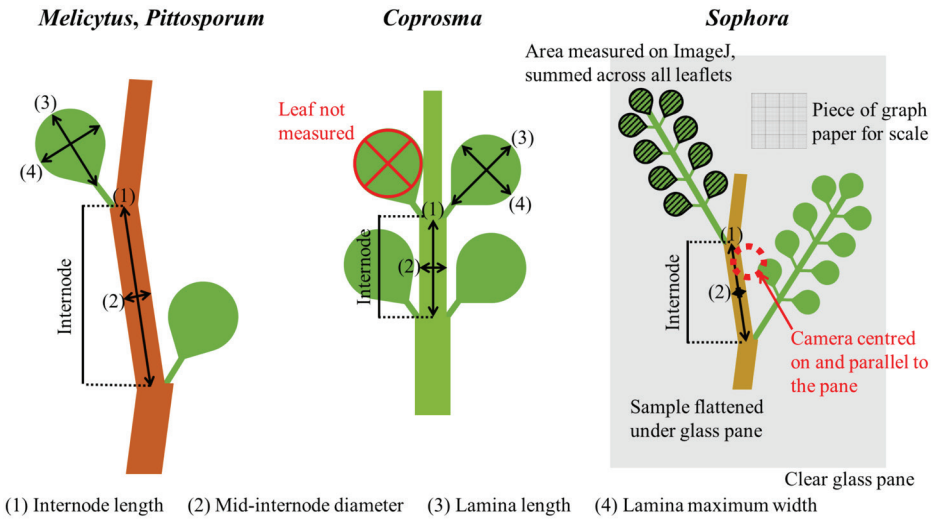
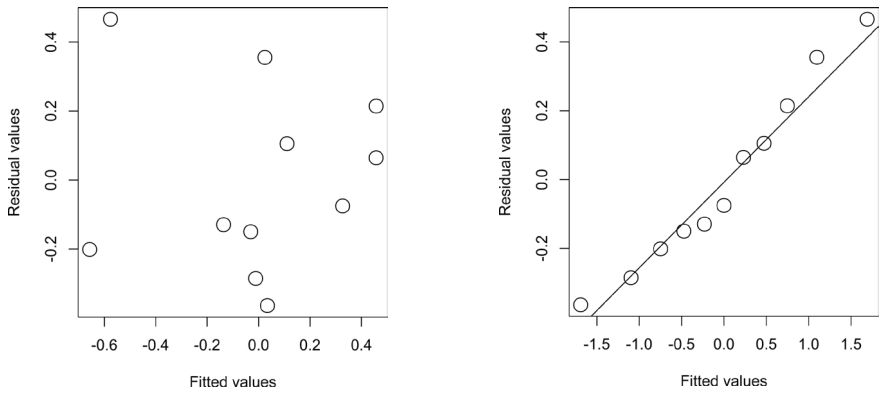
Appendices



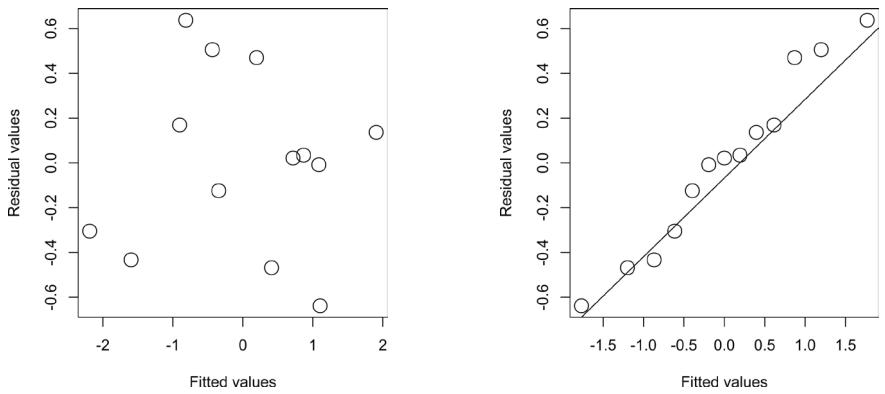
Appendix 1. Sketch explaining how we took the different measurements on our samples (see text in Material and methods).

Residuals plotted against fitted values | **Residuals plotted against normal quantiles plot (QQ plot)**

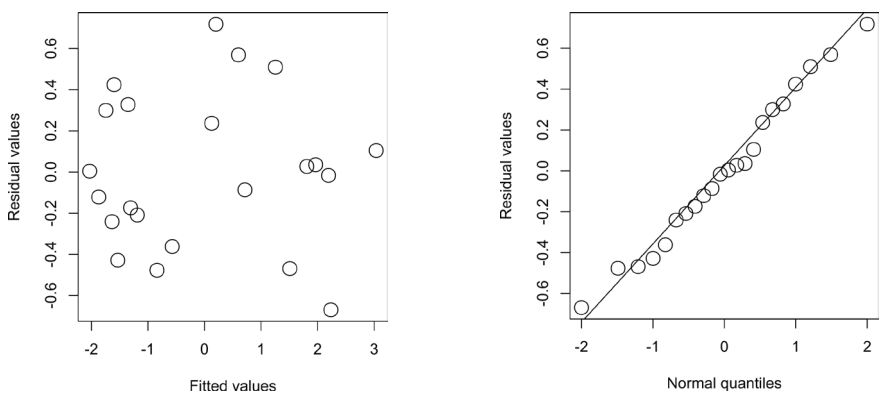
SMA with all the species – Plot for the divaricate species group



SMA with all the species – Plot for the non-divaricate species group



SMA without the leverage species – Plot for both groups combined (because the SMA analysis did not detect a difference between the two groups, the residuals of both must be fitted in the same diagnostic graphs)



Appendix 2. Distribution of the residuals of our SMA analyses.